

A Review of the Living Leptonacean Bivalves of the Genus *Aligena*

BY

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(40 Text figures)

IDENTIFYING A SPECIES OF *Aligena* from Galveston, which proved to be undescribed, led to the present review. I have reappraised all Recent species named in the genus or referred to it. Possibly other species will soon be found to belong here, for many of the descriptions and illustrations of leptonid bivalves in the literature are tantalizingly vague with regards to critical characters of the shell, and their generic allocations are questionable.

I am grateful to Mr. Cornelius Mock and Mr. Charles Guice of the U. S. Bureau of Commercial Fisheries, Galveston, for aid in field work and much useful material. Dr. J. P. E. Morrison, Dr. Harald Rehder and Dr. Joseph Rosewater, as well as the whole staff of the Department of Mollusks of the U. S. National Museum were very generous in aiding my studies there. This study was supported in part by National Science Foundation Grant GB 2753.

Aligena H. C. LEA, 1846

The genus *Aligena* H. C. LEA, 1843, when proposed, contained but two species of fossil bivalves from the Miocene beds of Petersburg, Virginia, *A. striata* and *A. laevis*, both nude names with neither designated as type. LEA described these species in 1846. In his synopsis of the Leptonacea of North America, DALL (1899) designated "*Abra aequata* CONRAD" as type of the genus. The following year he published a monographic account of *Aligena* (DALL, 1900: pp. 1175 - 1177), in which he noted that CONRAD's species was originally named *Amphidesma aequata* CONRAD, 1843, and that this is a senior synonym of *Aligena striata* H. C. LEA, 1846. *Kelliopsis* VERRILL & BUSH, 1898, type by monotypy *Montacuta elevata* STIMPSON, 1851, was considered a subjective synonym of *Aligena* by DALL (1899, p. 895; 1890, p. 1175). In this

he is probably justified, for the type species of *Kelliopsis* differs from the type of *Aligena* chiefly in being smaller, more quadrate, and in having weaker sculpturing. I have not had the opportunity to examine specimens of 2 other nominal genera based on Tertiary fossils of Europe, which DALL (1900) cites as congeneric (*Laubriera* COSSMANN, 1887) or closely related (*Spaniodon* REUSS, 1867).

Several additional living species have been added to *Aligena* in the twentieth century. *Aligena cerritensis* ARNOLD, 1903 was described from a Pleistocene deposit in southern California and has since been found living, chiefly south of there. *Aligena borniana* DALL, 1908 from deep water in the mid-Pacific is doubtfully a member of the genus, and *A. pisum* DALL, 1908, from the Strait of Magellan, is generically misplaced. *Aligena cokeri* DALL, 1909 from Peru is a member of the genus, as is *A. nucea* DALL, 1913 from the Gulf of California.

THIELE (1935) noted that *Aligena* differed so slightly from *Montacuta* that he was only doubtfully willing to recognize it as a subgenus therein. He pointed out that most living *Aligena* were on the shores of the American continents, but he also suggested, correctly, that *Montacuta salamensis* JAECKEL & THIELE, 1931 (in THIELE & JAECKEL, 1931) from the east coast of Africa might be an *Aligena*.

Two more species have recently been added to the list from the eastern Pacific, *Aligena redondoensis* T. BURCH, 1941, and *A. borealis* COWAN, 1964. For reasons noted below, these probably belong elsewhere.

The nondescript bivalves which are usually cited in the superfamily Erycinacea or Leptonacea are so poorly known that the allocation of genera to families is a complex question, which cannot yet be fully decided. For the present we may place *Aligena* in the Montacutidae, and define the genus as follows.

DEFINITION OF THE GENUS *Aligena*

Shell equivalve, small, 1 cm or less in maximum dimension; color always uniformly white; shape various, but usually the height and length are about the same; umbos touching, slightly prosogyrous, located midway the length or behind it, or rarely before it. There is no lunule, escutcheon or corcelet. The dorsal margins do not project across the midline. Outer surface sculptured only with growth lines, which may be very faint, or moderately pronounced, regular in size and spacing or irregular in those characters. Adductor scars are about equal in size, subquadrate to suboval; the pedal retractor scars join the adductor scars above (or are separated from them slightly, perhaps depending on stage of growth). Pallial line simple, without sinus, joining the ventral end of the adductor muscle scars, usually with ragged margins, at least on the upper side, and often discontinuous in one or several places. Valve margin thin and smooth. Umbonal cavity deep, the hinge plate very narrow, usually with a finger-like tooth below the umbo in each valve, of which the right one is slightly larger than the left. Lateral teeth are always absent. Ligament consisting of a thin, external part (tensilium) on the very margin of the shell following its curvature and extending before and behind the umbos, and a larger, straight, elongate internal part (resilium) which is entirely separated from the tensilium. The resilium extends in a straight line from immediately below the umbos for a moderate distance backward, and is therefore entirely opistodetic. Its attachments, or resilifers, are usually buttressed by a moderate thickening of the shell, or chondrophore, often terminated behind in a sharp angle. The resilifers diverge outward and downward from the umbos, and thus the resilium is narrow in front, broader behind, with the form of an elongate triangle in ventral view. The ventral surface of the resilium may be calcified, forming a lithodesma. The protoconch is oval, smooth, large (about 0.3 to 0.4 mm long) and remarkably persistent, being plainly evident in most large shells which are not worn. The periostracum is thin or moderately thick, light tan, usually with a smooth outer surface. It is only moderately persistent in most species.

In some species there is a vague, shallow sulcus on the disc of the valve, running from the umbo to the mid-ventral margin, and a corresponding sinus in the latter. Such species are slightly reniform in profile. This sulcus and marginal sinus are found in several other genera of the Leptonacea.

The species of *Aligena* as presently restricted are marine, mostly living from the lower tide level to shallow depths of perhaps 40 fathoms along the temperate and tropical shores chiefly of the American continents. One species of the Indo-Pacific fauna extends to greater depths. None are known from the eastern Atlantic or Antarctic faunas.

Although a few species of Leptonacea may be free living, most seem to be commensal with burrowing invertebrates, chiefly crustacea, polychaete worms and echinoderms. Nothing definite is known about the habits of most species of *Aligena*, but *A. cokeri* and possibly *A. texasiana* are probably polychaete associates.

TYPE SPECIES OF THE GENUS *Aligena**Aligena aequata* (CONRAD, 1843)

(Figures 1, 2, and 3)

Amphidesma aequata CONRAD, 1843. Proc. Acad. Sci. Philadelphia 1:307. Not figured. Type locality: St. Mary's Co., Maryland, and Wilmington, North Carolina. (Miocene)

Aligena striata H. C. LEA, 1846. Trans. Amer. Philosoph. Soc., 2nd Ser. 9: 238; pl. 34, fig. 13. Type locality: Tertiary beds of Petersburg, Virginia. (Miocene, *vide* DALL)

Aligena aequata CONRAD, 1843. DALL, 1900, Trans. Wagner Free Inst. Sci. 3 (5) : 1175; pl. 24, figs. 8, 8a, 8b (of vol. 3, no. 4).

The following description is based on a single left valve which is lot No. 144173 of the U. S. N. M. Paleontological Collection. It is labeled "St. Mary's River, Md., Miocene."

Shell subtriangular, dorsal margins only slightly convex, of about equal length, sloping abruptly at about the same angle. Ends and ventral margin evenly rounded. Umbo moderately inflated, protoconch large (but too indistinct to measure), located midway the length of



Figure 1

Aligena aequata CONRAD. Hinge of the specimen, USNM 144173, from the Miocene of Maryland, which Dall studied

the valve, and slightly turned forward. Curvature of the disc even, slightly flattened over the middle, but with no trace of a sulcus, nor any appreciable expansion of the anterior slope. No lunule, escutcheon or corselet. Sculpt-



Figure 2

Interior of valve of same shell as Figure 1. Length 9.93 mm

ture of numerous, closely spaced growth rests, of unequal size, but periodically enlarged to form small concentric ridges. Valve thin for its size, inner margin smooth. Hinge plate narrow, with a single finger-like tooth below the umbo in this, the left valve. The tooth projects well across the midplane. The resilial and tensilial parts of the ligament may have been completely separated, with the latter running along the very margin, where a nymphal roughening is evident. The inner part attached along a resilifer which begins below the umbo, and diverges ventrally and laterally. The chondrophore is very thickened, ending in a rounded point too far from the median plane to be a tooth. Length (extrapolating for the broken end) 9.93 mm; height 8.78 mm; semi-diameter 2.84 mm.

Another lot, U. S. N. M. 112378, labeled "*Aligena aequata* CONRAD from the Pliocene, Waccamaw River, South Carolina", consists of a left and a right valve much



Figure 3

Exterior of valve of same shell as Figure 1

better preserved than the lot from the Maryland locality. These valves are perhaps the ones figured by DALL, 1898, pl. 24, figs. 8, 8a, 8b. The ridges on the specimens are regular, but not quite as strong as he has shown them. They have no differentiated nymphal attachment for the tensilium, and the hinge plate is narrower than that of the valve from the Maryland Miocene.

To evaluate the relationship of *Aligena* to *Montacuta* TURTON, 1822, specimens of *M. substriata* MONTAGU from the Jeffreys collection at the National Museum were studied. This species, originally named *Mya substriata* MONTAGU, 1808, is the type species of *Montacuta* TURTON, 1822 by subsequent designation of GRAY, 1847. I have not seen Montagu's work, but according to FORBES & HANLEY (1850, 2: 77), the species was published in the supplement, which appeared in 1808 (*vide* PALMER, 1958, p. 312).

Montacuta substriata (MONTAGU, 1808)

(Figures 4 to 7)

The shell is minute (2.97 mm long, 2.84 mm high, 0.79 mm semidiameter), thin, obliquely ovate, with the anterior end longer than the posterior. The umbos are scarcely inflated, touching, and essentially orthogyrus. The protoconch is persistent, small and oval (0.125 mm long). Equivalve, with the disc moderately and regularly inflated, somewhat polished, with a few widely spaced



Figure 4

Montacuta substriata (MONTAGU). A specimen from Zetland in the Jeffreys collection (USNM 170517). Length 2.97 mm

growth rests. Major sculpture is of 3 to 10 widely spaced, faint radial lines, slightly elevated, most prominent on the middle third of the disk and toward the ventral margin. Valve margin smooth and sharp; pallial line wide, without a sinus and with even margins, joining the

adductor muscle scars at their lower ends. Adductor scars about equal in size, irregularly elongate, and with dorsal projections which are probably the scars of the pedal retractor muscles. Hinge short, with a single tooth in each valve. The teeth are rounded, elongated ridges beginning under the umbos and extending forward. That of the right valve is larger, and the tooth at the left



Figure 5

Interior of same valve as in Figure 4

valve fits in a shallow, poorly defined socket in front of and above the right one. A tensorial part of the ligament, if present, must be small and without noticeable attachment on the shell. The resilium is a flat ribbon, its attachments beginning at the umbo and sloping downward and laterally. The mid-ventral part of the resilium is a calcified strip.

Thus, the resilium is very similar to that of *Aligena*, which it also resembles in lacking lateral teeth, lunule and escutcheon. But these negative characters are outweighed by the differences between this species and *Aligena aequata*: *Montacuta substriata* is a much smaller shell, with small protoconch and umbos orthogyrous rather

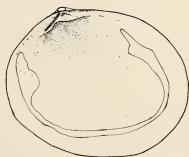


Figure 6

Interior of left valve of same shell shown in Figure 4

than prosogyrous. Growth striae are so poorly developed that the surface appears polished, whereas all species included in *Aligena* as here defined and limited, have moderate to prominent growth striae, giving the shell a silky texture, or even expanded to form concentric ribs. The pallial line in *Montacuta* is smooth and continuous, but the dorsal margin is ragged in all species of *Aligena* in which I have been able to study it. The radial sculpture of *Montacuta* is lacking in *Aligena*, and there is no finger-like projection of the teeth which are nearly always present in *Aligena*.

Another species of the eastern Atlantic generally included in *Montacuta*, *M. ferruginosa* (MONTAGU, 1808), has finger-like cardinal teeth projecting normal to the median plane of the shell, as well as low lamelliform bases of these teeth, continuing forward along the hinge plate. This may be why THIELE (1935) included *Aligena* in *Montacuta*. *Montacuta ferruginosa* is an elongate shell, with smooth surface, smooth margined pallial line, small size and orthogyrous protoconch, thus showing similarities to *M. substriata*. Its resilium is somewhat shorter than in *M. substriata*, the attachments diverging downward and outward more abruptly, so that it approaches the transverse ligament of *Mysella*. The differences in anatomy of the soft parts between *Montacuta substriata*



Figure 7

Ventral view of the hinge line of a shell of *Montacuta substriata* from the same lot as Figure 4, which had been fortuitously broken in such a way that the interlocking of the teeth and the resilium, with lithodesma, can be seen

and *M. ferruginosa* as detailed by OLDFIELD (1961) are, when considered in conjunction with differences in the shell, sufficient to suggest that the two species may ultimately be placed in different genera.

The loss of teeth may be a secondary character within the leptoid bivalves, which has occurred several times independently. At least one true *Aligena*, *A. cokeri*, is consistently edentate. We may suppose that ancestral populations may have had true lateral teeth (i. e. no projections of one valve margin below the other) and a cardinal tooth in each valve which had an elongated base extending forward under the hinge margin, with a digitiform projection normal to it at its umbonal end. The lateral teeth were lost in some later populations (including *Montacuta* and *Aligena*), the digitiform process lost in

M. substriata (but retained in *M. ferruginosa*), the elongate base lost in most *Aligena*, but not *A. cokeri* and *A. (?) borniana*.

Montacuta substriata and *M. ferruginosa* are the only two species recognized in that genus by WINKWORTH (1932) in his list of British Marine Mollusca. A third species was included with doubt. According to FORBES & HANLEY (1850), *M. ferruginosa* is known only from British seas, and lives subtidally to at least 30 fathoms. *Montacuta substriata* was known to them from Britain and Scandinavia, but not southward. They report it from depths of 5 to 140 fathoms. OLDFIELD (1961) gave an extensive anatomical account of both species, and noted that they are commensals on sea urchins. Insofar as comparison is possible, there are few significant differences in the anatomy of the soft parts of *M. substriata* and *Aligena texasiana* (see below).

SPECIES OF THE WESTERN ATLANTIC

Aligena elevata (STIMPSON, 1851)

(Figures 8 and 9)

Montacuta bidentata "TURTON 1822" of GOULD, 1841, Invert. Mass. Ed. 1, p. 59, not of TURTON (whose species is *Mya bidentata* MONTAGU, 1803, now placed in *Mytella*).

Montacuta elevata STIMPSON, 1851. Shells of New England, p. 16 (merely renamed the species misidentified by GOULD).

Kelliopsis elevata STIMPSON, 1851. VERRILL & BUSH, 1896, Proc. U. S. Nat. Mus., 20: 784; pl. 93, figs. 2-4; pl. 94, figs. 7, 8.

Aligena elevata STIMPSON, 1851. DALL, 1899, Proc. U. S. Nat. Mus. 21: 879, 884; 1900, Trans. Wagner Free Inst. Sci., 3 (5): 1177.

The shell is small (length 5.84 mm, height 4.75 mm, diameter 3.34 mm), equivalve, moderately inflated, oval to subtriangular, with the umbos moderately prominent, slightly closer to the hind end, and distinctly prosogyrous. The dorsal and ventral margins are only slightly convex, the front and hind margins more strongly rounded. The disc is evenly convex, with no median sulcus. Sculpture of fine, somewhat irregular growth lines, giving the shell a silky texture. There is a very thin, light tan periostracum. The protoconch is oval, about 0.4 mm long.

The hinge line is narrow, with a prominent finger-like cardinal tooth, projecting normal to the median plane. The resilifer is typical of the genus, and a tensilium attaches to the very margin of the shell over it. The dorsal margin of the broad, simple pallial line is ragged.

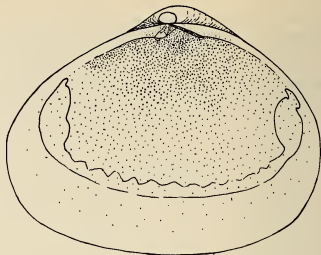


Figure 8

Aligena elevata (STIMPSON), interior of a right valve from Chelsea Beach, Massachusetts (USNM 159288). Length 5.81 mm

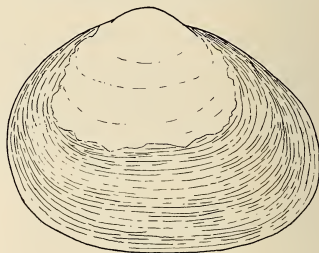


Figure 9

Exterior of same valve as Figure 8

This species is represented in the National collection from 16 lots ranging from Massachusetts to Long Island, from the shore to 10 fathoms.

Aligena texasiana HARRY, spec. nov.

(Figures 10 to 14)

Shell small (length 4.81 mm, height 3.75 mm, diameter 2.50 mm), white, chalky, moderately inflated; equivalve, sculptured only with numerous, irregularly spaced, fine

growth lines. Subtriangular to suboval or subquadrate, almost equilateral, the beaks being slightly closer to the hind end, but distinctly turned forward. The dorsal margins are very slightly convex, the hind one somewhat shorter than the front one. Both the front and hind ends of the shell are evenly rounded, and of nearly the same

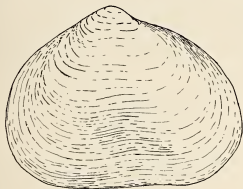


Figure 10

Aligena texasiana HARRY, spec. nov. Holotype. Length 4.81 mm

convexity. They continue as a smooth curve into the ventral margin, which is almost straight, but shows a slight sinus midway its length, at the end of the sulcus. The region of the disc between the umbo and antero-ventral part of the margin is somewhat more inflated than the rest of the disc. From the umbo to the middle of the ventral margin is a shallow, vague sulcus, only prominent on the lower half of larger shells. The protoconch is prominent, oval, about 0.348 mm in diameter.

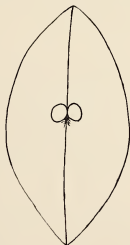


Figure 11

Aligena texasiana HARRY, spec. nov. Holotype

The umbos touch, and there is no lunule or escutcheon. The valves are thin, with smooth inner surfaces and margins. Adductor scars are prominent, suboval, and about equal in size. Retractor scars are adjacent or confluent (depending on growth) with them dorsally. The pallial line is prominent, without sinus, and broken into a series of subtriangular marks probably representing discrete muscle bundles. The resilium is flattened, short, attached by its long edges to each valve, along a slight ridge just under the dorsal valve margins and behind the umbos. The resilial attachments descend and diverge posteriorly. The medial third of the ventral surface of the resilium is calcified along its axis. There is a single tooth in each valve, rounded and projecting slightly forward across the midline. The one in the right valve is larger, and passes in front of the left tooth. A thin, light tan periostracum on fresh shells gives them a satiny luster.

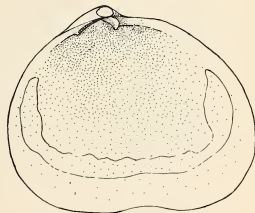


Figure 12

Aligena texasiana HARRY, spec. nov. Paratype, Length 5.13 mm

Type Locality: East end of West Bay, Galveston, Texas. The holotype is USNM no. 679103. This species has been found only in West Bay and Lower Galveston Bay at Galveston. It was not found in more than 60 samples ranging from 3 to 18 fathoms offshore. Within the bays, it occurs from the lowest tide level to 7 feet, which is about the deepest water of the bays, outside of the passes and dredged channels. It seems to be only local within the bays, and is not common. Frequently polychaetes are abundant in the samples containing it, suggesting it may have some mutualistic relationship with them, but details are lacking. It also occurs with *Mysella planulata*, with which it is easily confused. The latter is more flattened, has opistogyrous umbos with a smaller protoconch, and is without a sulcus on the disc. PARKER (1959, pp. 2128-

2129) evidently confused them, labeling a figure of *Ali-gena texasiana* with the name "*Mysella planulata*" (*l. c.*, figs. 21a, 21b). His specimens were from bays farther south on the Texas coast, but no exact localities are indicated. This species also occurs in Barataria Bay, Louisiana, where I recorded it as *Ali-gena* sp. (HARRY, 1942).

From *Ali-gena elevata*, this species differs in being generally smaller, more inflated, and with a median sulcus on the disc. *Ali-gena texasiana* is perhaps closest to what I have called *A. nucea* DALL from the west coast of Mexico, but the latter is not as inflated and the sulcus is less prominent. The Texas species is smaller than *A. cokeri*, with the sculpture and sulcus not as prominent, and cardinal teeth seem always to be present.

ANATOMICAL NOTES

In the laboratory, *Ali-gena texasiana* is moderately active, extending the foot and pulling its body, resting on its side, up to it. It crawls up the vertical wall of the glass dish, and up large shell fragments, attaching itself very loosely by a minute byssal thread or two. In the active animal, the siphonal opening is not evident, and my study did not extend to the direction of water currents. The mantle margin is exposed along the edge of the shell only to show a row of minute, closely spaced papillae, scarcely longer than their diameter, uniformly distributed along the edge of both mantle lobes between the adductor muscles.

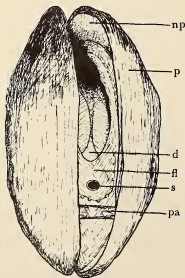


Figure 13

Ali-gena texasiana HARRY. Postventral view of an animal from which the shell has been decalcified

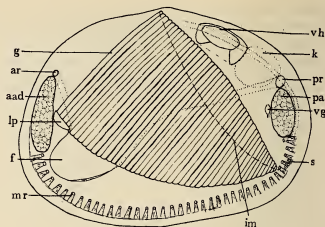


Figure 14

Ali-gena texasiana HARRY, spec. nov.

Diagram of the superficial anatomy of a specimen from which the shell has been removed

Symbols used in Figures 13 and 14:

aad	anterior adductor muscle
ar	anterior pedal retractor muscle
d	diaphragm
f	foot
fl	fused lamellae of mantle margin
g	gill
im	dorsal margin of ascending gill lamella
k	kidney
lp	labial palp
mr	retractor muscle of mantle margin
np	nascent periostracum
p	periostracum
pa	posterior adductor muscle
pr	posterior pedal retractor muscle
s	siphonal opening (excurrent)
vg	visceral ganglion
vh	ventricle of the heart

The flesh of the living animal internally is snow white, except that the liver is colored light brown, and the kidney is faint tan. A byssal gland is not evident in the living animal, but there is a groove along the keeled ventral margin of the foot. The foot is somewhat finger-shaped, although short and rounded when retracted.

Studies on specimens preserved in 70% isopropyl alcohol were made after the shell was dissolved in a very weak hydrochloric acid (2%) solution in alcohol of 70% strength. The outer, or true, periostracum is thin, transparent, light tan colored, with a roughened outer surface in harmony with the growth ridges of the shell. The free edge of this layer of periostracum is held firmly in the periostracal groove between the outer and middle lamellae of the mantle margin. Since the latter has re-

tracted some distance from the shell margin, there is an abrupt turning of the outer periostracal sheet, along the line of the shell margin, and a wide strip of nascent periostracum between it and the mantle margin.

An inner periostracal sheet seems to adhere closely to the outer surface of the mantle in specimens deshelled in acid, but it was probably separated from the mantle by the innermost layer of calcareous material, the hypostracum. I therefore propose for this sheet of periostracum the name mesostracum. In *Aligena texasiana* it is smooth, tough, pliable, thin, and very faint tan colored. It seems to extend to the very margin of the mantle.

The margins of the two mantle lobes are fused for a short distance below the posterior adductor muscle. The fusion is in the form of a thin, transverse sheet, with a large round hole at its upper end. This hole has a smooth margin and is the excurrent siphonal opening. The papillae extend along the sides of the sheet, and the two rows of them join above the siphonal opening.

The mantle margin is thickened, but the rest of the mantle is very thin, almost transparent. Discrete bundles of retractor muscles can be seen in it, extending upward for a short distance, and originating on the valves of the shell along the pallial line.

The gills are represented only by a single huge subtriangular demibranch on each side. There is no muscular suspensory septum. Each demibranch has about 50 filaments, the longest being anterior, and the others shortening in length progressively toward the hind end. The lamellae are not pleated. They are eulamellibranchian, with firm inter-filamentary junctions orderly arranged horizontally to give the gill a latticed appearance (not shown in Figure 14). The free margins of the demibranchs are grooved. The anterior filament of each is attached along the visceral mass throughout its length. The ascending lamellae are somewhat narrower than the outer, descending ones. They attach along the visceral mass in the front part of the gill, and behind it to each other. The hind tips of the gills do not reach quite to the siphonal opening, but there is a triangular, horizontal sheet of tissue extending from the hind tip of the gills to the fusion of the mantle lobes just below the opening. Thus, the mantle cavity is completely separated into incurrent and excurrent chambers by a structurally complete diaphragm.

The labial palps are minute triangles, which overlap only the first few filaments of the gill. The ventricle of the heart surrounds the rectum, the kidney is between the pericardium and the posterior adductor muscle.

No internal detail of the viscera has been determined. On the surface of the visceral mass, there were a few low projections, which could as easily be interpreted as

phenomena of contraction rather than as projections of the liver and gonads. The latter condition has been described in other leptonids (OLDFIELD, 1961).

A specimen collected in early spring had several hundred early embryos in the gills, but there was no evidence of embryos in specimens examined in June and July. OLDFIELD (*op. cit.*) describes a sequential shift in sexuality of some British leptonids.

SPECIES OF THE EASTERN PACIFIC

Aligena cerritensis ARNOLD, 1903

(Figures 15 to 17)

Aligena cerritensis ARNOLD, 1903. Mem. Calif. Acad. Sci. 3: 138; pl. 13, fig. 3. Type locality: Los Cerritos (Signal Hill) near Long Beach, Los Angeles County, California. (Pleistocene)

The following description is based on the holotype USNM 162529, a single right valve (Figure 15).



Figure 15

Aligena cerritensis ARNOLD.
Holotype, USNM 162529. Length 9.03 mm

Shell large for the genus (length 9.03 mm, height 8.39 mm, semidiameter 2.58 mm), obliquely ovoid, the posterior dorsal margin sloping downward at a greater angle with the horizontal than the anterior dorsal one. The shell is unusually thick, and the inside of the disc, above the pallial line, has an irregular surface. The chevron-shaped origins of the pallial retractor muscle give the upper part of the pallial line an irregular appearance. These are actually engraved on the thickening of the disc. The adductor scars seem to be large and slightly kidney-

shaped. The resilifer is as in *Aligena*, and the shell ridge along it is large. There is a single, finger-like tooth in front of the ligament in this, the right valve, projecting normal to the midplane and across it. Outer surface slightly flattened over the middle of the disc, smooth, with only a few irregular growth rests on the lower third of the shell. No lunule or escutcheon.

This species is living on the coast of Lower California and on the mainland opposite. Some of the 14 lots of



Figure 16

Aligena cerritensis ARNOLD

A Recent shell from "off Lower Calif." USNM 212588 to show the steep slope of the postdorsal margin. Length 5.63 mm

this species in the National Museum have depth data, showing it occurs in from $\frac{1}{2}$ to 5 fathoms, and in fine grey or black sand. It may occur with *Aligena nucea*. Fresh shells are rarely as thickened as the holotype. They often have a periostracum which is much thicker than on any other species of *Aligena*, and which may persist only over the lower third of the shell. It is brownish grey in

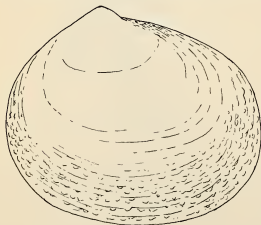


Figure 17

Aligena cerritensis ARNOLD

A Recent shell from Magdalena Bay, Lower California (USNM 217809) showing papillate periostracum over lower third of valve. Length 5.00 mm

some shells, light tan on others, and usually has small triangular projections from its surface. Figure 17 is drawn from a Recent shell having such a cuticle. The protoconch is large. The shape is variable, and small shells are difficult to separate from *A. nucea*. The beak cavities are not as deep as in that species, there is never a sulcus on the disc, and the ventral margin is always slightly convex, never having a sinus. The umbos are always well toward the hind end of the shell.

Aligena obliqua HARRY, spec. nov.

(Figures 18 to 20)

Shell small (length 6.19 mm; height 6.19 mm, at right angle to length; diameter 2.38 mm; protoconch oval, 0.284 mm long), white, covered with a light tan, very thin periostracum. Moderately and regularly inflated, obliquely oval, with the margins evenly rounded. Equivalve, inequilateral, with the umbos about a third of the

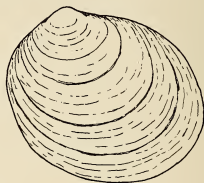


Figure 18

Aligena obliqua HARRY, spec. nov.

Holotype, USNM 532795. Length 6.19 mm

length from the hind end. Umbos only moderately inflated, turned slightly forward, touching, with persistent protoconchs. No lunule or escutcheon. Sculptured only with growth striae, faint, close together, and mostly regular, with occasional (3 on holotype) growth rests more prominently defined. The growth striae give the surface a silky texture. Valves of moderate and even thickness, margin smooth and sharp, adductor muscle scars very elongate oval, with the foot retractor scars confluent with their dorsal ends. Beak cavities deep, hinge very narrow. A single prominent finger-like tooth arises just in front of the umbo in each valve, projecting well across the midline. The tooth of the right valve is larger than that



Figure 19

Aligena obliqua HARRY, spec. nov.
Holotype, interior of valve

of the left, more directly under the umbo, and it passes behind the left when the valves are joined. Ligament with a thin, external part on the very margin of the shell, and of the same length as the resilial part. The latter begins under the umbo, its attachment slopes downward and laterally, for not quite half the distance from the umbo to the top of the posterior adductor scar. The ventral surface of the resilium is strongly calcified. The shell is thickened slightly along the resilial attachment.

Holotype, USNM no. 532795, is from Bacochibampo Bay, Sonora, Mexico (Orcutt). This lot also contains 2 paratypes with joined valves and 10 disjoined valves. All are in fresh condition, showing little evidence of weathering.

The distinctive shape of this species easily separates it from the other 3 living on the west coast. It is very similar

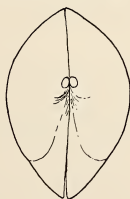


Figure 20

Aligena obliqua HARRY, spec. nov.
Dorsal view of a paratype from same lot as that of Figure 18

to *Aligena minor* DALL (1900, p. 1177, pl. 44, fig. 8), a Miocene species from North Carolina, which differs chiefly in being smaller, and not as oblique.

The National Museum has 6 lots of this species, from Guaymas (Sonora) and Mazatlan (Sinaloa) on the main-coast of the Gulf of California. Depths are indicated on the labels as $\frac{1}{2}$ to $1\frac{1}{2}$ fathoms, and substrate type of medium-coarse grey sand.

Aligena nucea DALL, 1913

(Figures 21 to 24)

Aligena nucea DALL, 1913. Proc. U.S. Nat. Mus., 45: 597.
Not figured. Type locality: Gulf of California. BURCH, 1941, Nautilus 55: pl. 4, fig. 3 (photograph of holotype).
OLSSON, 1961. Panamic-Pacific Pelecypoda, p. 254; pl.

The single left valve, which is the holotype of this species (USNM no. 267149), is probably a more extreme variant of the populations which I think constitute this species than is ordinarily found in populations of *Aligena*. A description of the holotype (Figure 21) is as follows:



Figure 21

Aligena nucea DALL. Holotype, USNM 267149. Length 3.88 mm

Shell small (length 3.88 mm, height 3.19 mm, semidiameter 1.31 mm), the umbo is very slightly behind the midpoint of the length, slightly prosogyrous, and evidently touched the one opposite. Protoconch large, persistent



Figure 22

Aligena nucea DALL. Dorsal view of holotype

but indistinct. Resilifer typical of *Aligena*, but unusually large and prominent. There is a single finger-like tooth just in front of the umbo. Sculpture of growth lines only, more prominent on the lower third of the valve. Disc



Figure 23

Aligena nucca DALL. Interior of valve from Conception Bay, Gulf of California (USNM 558735). Length 5.63 mm

curvature uniform, with no flattening or sulcus. Ventral margin evenly rounded, with the post-ventral part slightly flattened. No lunule or escutcheon.

It differs from *Aligena cerritensis* of the same length in having a more swollen umbo, which is more centrally placed. *Aligena obliqua* of this size is already markedly oblique. From *A. cokeri* it differs in being dentate. Several lots of specimens have accumulated in the National Museum since Dall named this species, which, though poorly represented by the holotype, seem nonetheless to be conspecific with it.

Figures 23 and 24 are drawn from a valve of USNM 558735 from Conception Bay, Gulf of California. The shell is about equally rounded at both ends, with the ventral margin flattened, or more often with a slight sinus in the middle. There is usually a vague, very shallow and broad sulcus on the lower half of the middle of larger valves, and the anterior slope of the disc sometimes is slightly inflated. The texture is silky, formed by very fine, closely spaced and somewhat irregular growth lines. The cardinal tooth is always present. The umbos vary in position, may be slightly in front or slightly behind the midpoint of the length.



Figure 24

Aligena nucca DALL. Exterior of same valve as in Figure 23

Eleven lots of this species at the National Museum are all from the Gulf of California, with depths indicated as 1 to 7 fathoms, and substrate as fine grey or black sand. OLSSON (1961) notes it extends south to Nicaragua.

Aligena cokeri DALL, 1909

(Figures 25, 26)

Aligena cokeri DALL, 1909. Proc. U. S. Nat. Mus. 37: 155-156; pl. 28, figs. 5, 6. Type locality: "Attached to worm tubes thrown upon the beach of the lagoon at Capon, Peru." OLSSON, 1961. Panamio-Pacific Pelecypoda, p. 234; pl. 33, figs. 6, 6a, 6b.

Shell small (Holotype, USNM 207759, length 7.74 mm, height 6.45 mm, diameter 5.68 mm), very inflated, ends of about equal curvature, rounded, ventral margin only slightly curved, and with a rounded shallow notch in the middle, where the sulcus ends. Beaks strongly prosogyrous, slightly in front of the midpoint of the length. Protoconch persistent and large (about 0.38 mm long, slightly oval). A vaguely defined, moderately wide furrow runs from the umbo to the midpoint of the ventral margin, is

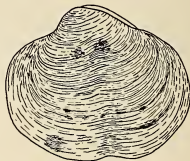


Figure 25

Aligena cokeri DALL. Holotype, USNM 207759. Length 7.74 mm

scarcely evident on the umbones, becomes more pronounced on the lower $\frac{2}{3}$ of the shell. Growth lines very prominent, standing up as small, sharp ridges, but somewhat irregular, though closely spaced; the shells tend to be peculiarly malcolated in some places, with vague, irregular depressions and elevations. In other lots than the type, the growth-line sculpture may be very regular or nearly absent, and the depressions and elevations absent, or variously prominent. In some specimens from the northern part of the range, the growth lines are absent, the bumps and hollows so pronounced and numerous that one might almost proclaim it a different species, were there no connecting intergrades. The form may become

subtriangular in these, and the sulcus on the disc be absent. The resilifer is typical of the genus; in some paratype shells with both valves connected, a tensilium is evident, but this is scarcely more than a slight thickening of the periostracum, joining the valves over the resilium. The finger-like tooth of *Aligena* is absent in this species,



Figure 26

Aligena cokeri DALL. Hinge of right valve of a syntype

which has a slight, rounded ridge running forward from the umbos along the hinge. The ridge of the left valve is smaller than that of the right one. Neither ridge projects across the median plane.

The edentulous condition was noted by DALL (1909) and OLSSON (1961, pl. 33, fig. 6) has illustrated it with a good photograph.

Besides the type lot, there are several others at the National Museum ranging from the Gulf of California to Panama. Some labels indicate depths of 1 to 4 fathoms.

SPECIES OF THE WESTERN PACIFIC AND INDIAN OCEANS

Aligena salamensis (JAECKEL & THIELE, 1931)

(Figures 27 to 29)

Montacuta salamensis JAECKEL & THIELE, 1931. Wiss. Ergeb. d. deutsch. Tiefsee-Expedit. 21 (1): 226; pl. 4, fig. 98.
Type locality: Dar es Salam, 50 meters deep.

THIELE (1935) noted that this species from the coast of East Africa might belong to *Aligena*. Several lots in the National Museum from southeastern Asia seem to fit it, insofar as comparison with the meager description and figure of JAECKEL & THIELE (in THIELE & JAECKEL, 1931) allow comparison.

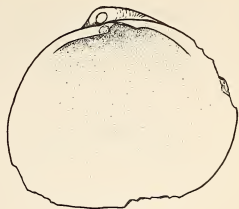


Figure 27

Aligena salamensis JAECKEL & THIELE.
China Sea, 230 fathoms, off Pratas Island. USNM 297075.
Length 9.42 mm

Shell small (length 9.42 mm, height 8.39 mm, semidiameter 3.57 mm), very inflated, subquadrate in profile, with margins evenly rounded. Beaks about midway the length, turned forward, touching, the protoconch oval, large, smooth, and persistent. Ventral margin slightly sinuous, where the sulcus of the disc meets it. The sulcus is prominent only over the lower half of larger shells, and the anterior slope of the shell is slightly more inflated than the rest of the disc. Sculpture of closely placed growth lines of uniform size, which become coarser on the lower half of the shell.



Figure 28

Aligena salamensis JAECKEL & THIELE.
Dorsal view of valve drawn in Figure 29

Valve thin, margin smooth and sharp. The hinge has a large fingerform tooth projecting below the umbo; the resilial attachment slopes downward and outward from the umbo, and is buttressed by a thickening of the shell along it, ending in a prominent angle at the hind end of the resilium.

Young specimens are evenly inflated and almost circular. They lack a median sulcus, and might be thought another species, were it not for connecting intergrades. The National Museum has 4 lots from the China Seas, off Pratas Island, ranging from 88 to 230 fathoms, and 7 lots from the Philippines, ranging from 10 to 37 fathoms. A

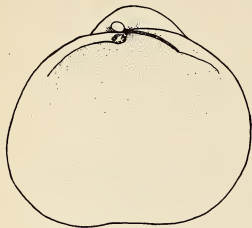


Figure 29

Aligena salamensis JAECKEL & THIELE.

A valve from 32 fathoms S. E. of Bantayan Island, Philippines (USNM 293038). Length 4.69 mm. This was drawn at twice the magnification of Figure 27

single lot from the Buton Strait, Celebes, is from 37 fathoms also. Most lots have only one or two valves, the maximum being six. All of the smaller shells are from the greater depths, but there are sufficient intergrades to demonstrate they are conspecific with the larger ones. These were collected in 1909 by the research vessel "Albatross."

This species seems to penetrate to greater depths than others in the genus, but its shell is very characteristic of *Aligena* in all respects.

SPECIES INCERTIS SEDIS

Aligena (?) *borniana* DALL, 1908

(Figures 30, 31)

Aligena borniana DALL, 1908. Bull. Mus. Comp. Zool. 43 (6): 413; pl. 10, fig. 2. Type locality: Pacific Ocean, 16°32' S latitude, 119°59' W longitude, 2012 fathoms.

Shell large for the genus (length 14.2 mm, height 10.3 mm, semidiameter 3.6 mm; protoconch oval, about 0.44 mm long), elongate oval, the front and hind margins evenly



Figure 30

Aligena (?) *borniana* DALL. Holotype, USNM 110585. Length 14.2 mm

rounded and of nearly the same arc, the ventral margin almost straight. Valves inflated, of the same size, beaks about $\frac{1}{3}$ the length from the hind end, prosogyrous and touching each other.

Very closely spaced growth lines and a light tan periostracum give the outer surface a silky texture. Growth lines are more prominent near the beaks than elsewhere. No lunule or escutcheon, but there is a narrow, vaguely defined sulcus on the posterior slope on the upper third of the shell only. The middle of the disc is slightly flattened, but shows no trace of a sulcus (contrary to Dall's description). No evidence of a tensilium on the disjoined

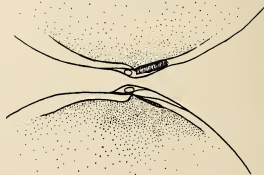


Figure 31

Aligena (?) *borniana* DALL. Hinge of holotype with resiliium attached to left valve

valves of the single available specimen, the holotype. The resilium is typical of *Aligena*, but seems not to have a calcified strip. The hinge line in front of the umbo is slightly thickened, more so in the right than in the left valve, but there is no finger-like projection, and neither thickening extends across the midplane. The adductor scars and pallial line could not be distinguished.

The relatively compressed appearance of this species, its large size, the faint sulcus on the posterior slope, as well as the great depth at which it occurs, are characters which, if relatively insignificant, argue against this species being an *Aligena*. The lack of a projecting tooth typical of most species of *Aligena* is not significant, since *A. cokeri* has no such tooth. This might be placed in *Montacuta*, except for the large size and the faint posterior sulcus. The latter suggests a corcelet, and thus the Thyasiridae, but the shape is unlike that group.

SPECIES REMOVED FROM *Aligena*

Three species have been described as *Aligena* which belong elsewhere. Two of these are probably Thyasiridae: *Aligena redondoensis* T. BURCH, 1941 and *A. pisum* DALL, 1908. The third, *A. borealis* COWAN, 1962 may belong to that family. The three are sufficiently distinct from each other to merit being placed in separate genera.

The smaller species of Thyasiridae may be covered with iron encrustation, a character which has not been found in *Aligena*, although it is known to occur in *Montacuta ferruginosa* (see OLDFIELD, 1961). The thyasirids, at least the smaller ones, are generally found at greater depths than most species of *Aligena*, and occur in cooler waters when living in shallow depths. A lunule, escutcheon and corcelet (see CARTER, 1967, for a discussion of these characters) may occur in various combinations and manifest to varying degrees in the Thyasiridae, but they are absent in *Aligena*.

Axinulus VERRILL & BUSH, 1898

Axinulus (?) *pisum* (DALL, 1908)

(Figures 32, 33)

Aligena pisum DALL, 1908. Bull. Mus. Comp. Zool. 43 (6): 413. Not figured. Type locality: "Magellan Strait, in 61 fathoms."

Only the holotype of this species, a slightly worn left valve, is known. In a large series at the National Museum of unidentified shells dredged near the Philippines by the "Albatross," there are a few valves which are very similar,

if not identical (USNM 300962, Lagonoy, G., E. Luzon, Philippines, 569 fms.). The following description is based on the holotype.

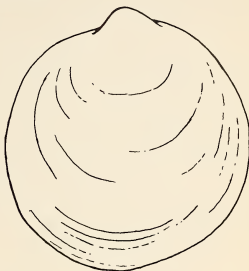


Figure 32

Axinulus (?) *pisum* DALL.

Holotype, USNM 110715. Length 2.43 mm

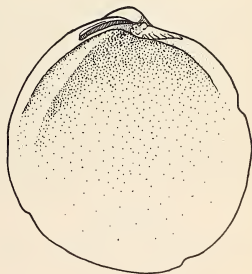


Figure 33

Axinulus (?) *pisum* DALL. Holotype, interior view

Shell small (length 2.43 mm, height 2.69 mm, semi-diameter 0.82 mm), subcircular, white and opaque with a very light tan, thin periostracum to which no dirt is adhering. Umbo moderately inflated, and slightly proso-

gyrous. The protoconch is scarcely evident, but seems to be slightly oval, about 0.156 mm long. The curvature of the disc is regular, with no lunule, escutcheon, or corcelet evident externally. Surface almost smooth, showing only a few very faint growth rests. The valve is thin, its edge smooth. Adductor scars and pallial line not evident. There is a faint but distinct ridge, ill-defined but fairly broad, extending from the umbonal cavity near the posterior dorsal margin, very suggestive of a corcelet. Hinge plate narrow, with no evidence of a tensilium, but with a resilifer beginning just under the umbo and sloping downward and outward for a moderate length. A single irregular tooth is immediately below and in front of the umbo. The hind part of the tooth may be a broken, finger-like projection, but it appears to have several rounded bosses, one of which is on the top side. A triangular extension forward of this tooth has a moderately sharp ventral border, along which are several incised lines sloping upward and backward.

Tomburchus HARRY, gen. nov. in Thyasiridae

Type Species: *Aligena redondoensis* T. BURCH, 1941.

Shells small, oval, equivalve, inequilateral, with the umbos nearer the hind end, and prosogyrous. An escutcheon is well defined by a sharp angle on the posterior slope, extending from the umbo to the hind end of the shell. No lateral teeth, but the postdorsal slope of the left valve extends under the margin of the right one. The left valve margin is also deflected under and just before the umbo, as a tooth-like lamella with bifid margin, passing under a small, rounded, tooth-like extension of the margin of the right valve. Ligament superficial, but covered by a turned up margin of the shell, extending along the adumbonal half of the escutcheon. The genus is named in honor of Dr. Tom Burch, of a family whose several members have greatly stimulated and furthered the study of malacology.

Tomburchus redondoensis (T. BURCH, 1941)

(Figures 34 to 37)

Aligena redondoensis T. BURCH, 1941. Nautilus 55: 50-51; pl. 4, figs. 5, 6, 7. Type locality: 75 fathoms off Redondo Beach, California, about latitude 33°38'50" W, longitude 118°26'30" N.

The paratypes of this species cited by T. BURCH (1941) as sent to the National Museum were misplaced and unavailable to me when I studied *Aligena* there in 1968. Two lots of the National collection identified by Dr. A.

M. Keen and cited by T. Burch were studied instead. One of these, USNM 211882 (48 fms., off Santa Rosa Id., Calif.) has only a single very worn valve, but is possibly this species. The other, USNM 331216a (129 fms., off La Jolla, Calif.), has two specimens which fit very closely the figures and description of *Aligena redondoensis*. The following description is based on that lot.



Figure 34

Tomburchus redondoensis (T. BURCH)
From 128 fathoms "off La Jolla, Calif." (USNM 331216a).
Hinge of left valve. Length 3.10 mm

Shell small (length 3.10 mm, height 2.53 mm, semidiometer 1.14 mm), oval, equivalve, inequilateral, with the umbos slightly closer to the hind end, moderately inflated and prosogyrous. Protoconch persistent, oval, about 0.158 mm long. Valves white, moderately inflated, sculptured only by fine growth lines, with a thin periostracum to which mud and iron deposits adhere tenaciously in a few places. The margin of the shell is formed by one continuous curve, somewhat more flattened anterodorsally and along the ventral margin, but closed by the more flattened segment of the postdorsal margin, which meets the ventral margin in a rounded angle, about halfway between the top and the bottom of the shell.



Figure 35

Tomburchus redondoensis (T. BURCH)
Top view of same valve as in Figure 34. The dashed line is the limit of the postdorsal margin inserted below that of the right valve

No lunule is differentiated. A narrow, lenticular escutcheon is well defined by a sharp margin and deeply excavated surface, which is pinched up into a keel along the umbonal half of the shell margin. There is no corcelet. The ligament seems to consist of one piece, with the tensilium and resilium possibly fused. It is about $\frac{1}{3}$ as

long as the escutcheon, and attached to the inner side of the pinched up part of the shell margins. It is effectively concealed by this keel. There are no lateral teeth as such, but in the left valve the posterior half of the dorsal margin within the escutcheon is extended across the me-

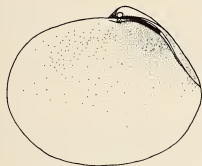


Figure 36

Tomburchus redondoensis (T. BURCH)
Right valve of same shell as in Figure 34

dian plane, and bent slightly downward. It fits under the margin of the right valve, which does not cross the median plane there. The margin of the left valve is also extended just before and under the umbo, as a flattened, bifid tooth. Seen from above, this "tooth" is narrow, elongate along the shell margin, with its free margin smoothly rounded. In the right valve there is a small, hemispherical extension of the shell margin, which does



Figure 37

Tomburchus redondoensis (T. BURCH)

Top view of a shell with valves joined, from same lot as Figure 34.
Darkened areas are detritus

not extend across the median plane, but fits in the notch of the tooth of the left valve. The adductor scars and pallial line could not be studied.

A few lots of unidentified shells at the National Museum, dredged near the Philippines by the "Albatross" in 1909, evidently are this species or a closely related one, but

the present study could not be extended to include them. Another member of *Tomburchus* may be *Axinus dubius* DAUTZENBERG & FISCHER, 1897 (10: 215 - 216, pl. 6, figs. 18 to 21; renamed *Thyasira dubia* (DAUTZENBERG & FISCHER) by DAUTZENBERG, 1927: 312 - 313, pl. 8, figs. 35 to 38) from the Azores, but I have seen no authentic specimens.

"*Lucina*" *ferruginosa* FORBES, 1843, as described and figured by FORBES & HANLEY (1850, 2: 60 - 62, pl. 34, fig. 1) from Britain may also be of this genus. WINCKWORTH (1932, p. 242) puts FORBES' species in *Thyasira*. VERRILL & BUSH (1898, p. 793, pl. 87, figs. 7, 8) cite what may be the same species as "*Cryptodon* (*Axinus*) *ferruginosus* (FORBES)", but they give no description and the figure has insufficient detail.

Odontogena COWAN, 1964

Odontogena borealis (COWAN, 1964)

(Figures 38 to 40)

Aligina (*Odontogena*) *borealis* COWAN, 1964. Veliger 7 (2): 108 - 109; pl. 20, figs. 1, 2. Type locality: Georgia Strait, British Columbia, Canada, 190 fathoms.

The following description is based on the single paratype, disjoined valves of one shell, which is USNM 657130.

Shell small (length 2.56 mm, height 2.37 mm, semi-diameter 0.63 mm), subcircular, resembling a minute *Lucina*, with slightly convex, long post-dorsal margin. The moderately convex shorter anterior margin meets the umbo in such a way as to give the dorsal margin a notched appearance. No lunule, escutcheon or corcelet. Inflated, and covered with a ferruginous deposit which had been mostly removed, to show a faint tan surface of silky texture with a few irregular growth lines as the only



Figure 38

Odontogena borealis (COWAN). Paratype, USNM 657130
Length 2.56 mm

sculpture. Beaks touching, slightly turned forward, about midway the length of the shell. Valves thin, the margin acute and smooth. Adductor scars and pallial line could not be made out. Hinge line very narrow, poorly manifest; ligament entirely internal, elongate, flattened, attached along its side to the valves, beginning at the umbos and extending a short distance behind; the attachments do not diverge posteriorly. Teeth two in each valve; these



Figure 39

Odontogena borealis (COWAN).

Right valve of same shell as in Figure 38

are large masses, poorly defined, as are the sockets into which they fit. One tooth in each valve is just under and in front of the umbo, the other is behind the ligament. Those in the right valve are bifid and receive in the vague groove thus formed a short rounded projection from the teeth of the left valve. The ligament does not appear to have a calcareous midstrip, but this could be a matter of age.



Figure 40

Odontogena borealis (COWAN).

Top view of shell in Figures 38 and 39

This species resembles *Aligena* of the east coast in type of ligament, general shape, texture and size of shell, and absence of lunule and escutcheon. The type of teeth, however, removes it from that genus, as characters in this group go, and the subgenus Cowan erected for it may be used unless an earlier name is found.

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